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Use of restoration-treated ponderosa pine forest by tassel-eared squirrels

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The tassel-eared squirrel (*Sciurus aberti*) is dependent on ponderosa pine (*Pinus ponderosa*) for food and cover and is likely to be affected by management treatments intended to restore currently dense ponderosa pine forests to presettlement, more-open stand structure. We used radiotelemetry to determine how restoration treatments affected habitat use by tassel-eared squirrels. Mean 50% fixed kernel core areas and 85% fixed kernel home ranges were significantly smaller in winter (core = 1.1 ha; home range = 5.1 ha) than nonwinter (core = 3.48 ha; home range = 13.81 ha), and squirrels selected untreated forests and areas with high (51–75%) canopy cover for these winter areas. During nonwinter core areas and home ranges expanded to include treated areas with high canopy cover (51–75%). Squirrels placed the majority of winter nests in areas with >51% canopy cover and high (0.0601–0.0819 kg/m^3) crown bulk density. Given the apparent importance of denser, untreated patches and treated areas with canopy cover of 51–75% in winter, we suggest retaining some areas with these characteristics where it is compatible with other forest management objectives.

Key words: Arizona, home range, *Pinus ponderosa*, restoration, *Sciurus aberti*

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Over the past 150 years ponderosa pine (*Pinus ponderosa*) forests of the American Southwest have shifted from relatively open, park-like stands with clumps of large-diameter (old-growth) trees (Cooper 1960; White 1985) to dense stands with many small-diameter trees and very little open area (Covington and Moore 1994). In part due to the threat these dense stands pose as foci for high-intensity wildfires, management of pine forests in the Southwest has shifted to restoring presettlement stand structure via mechanical thinning and returning low-intensity fire at intervals appropriate to this fire-adapted landscape (Allen et al. 2002). This approach can reduce basal area by up to 66%, reduce trees per acre by up to 88% (Fulé et al. 2001), and allow the herbaceous understory to reestablish (Moore et al. 2006). Although these treatments can create tree densities and spatial patterns resembling those present during presettlement, most restored stands will require considerable time to develop a dominant old-growth tree component. Consequently, restoration could alter habitat quality for mammals associated with ponderosa pine forests for an extended period after treatment.

The tassel-eared squirrel (*Sciurus aberti*) is dependent on ponderosa pine for both food and cover (Dodd et al. 2003; Farentinos 1972; Keith 1965). This squirrel's diet is composed almost exclusively of ponderosa pine tissue (seeds, cones, and inner bark) or plants and fungi closely associated with ponderosa pine (Austin 1990; Keith 1965; Snyder 1992; States et al. 1988; Stephenson 1975). Tasseled-ear squirrels build both winter and nonwinter nests exclusively in the upper branches of large (37.5- to 57.5-cm diameter at breast height [DBH]) ponderosa pines (Halloran and Bekoff 1994; Snyder and Linhart 1994). Although squirrels depend upon the pine throughout the year, winter is especially critical, because their primary winter food source is the inner bark of pine twigs (Hall 1981; Keith 1965) collected from a subset of trees that differ in mineral and terpene concentration from trees not fed upon (Farentinos et al. 1981; Snyder 1992; Zhang and States 1991). The chemical composition of feed trees is not correlated with obvious physical attributes of the tree (Farentinos et al. 1981), but differences apparently can be detected by squirrels, because trees are consistently used from year to year (Hall 1981; Keith 1965). These feed trees are typically found in clumps that are distributed throughout a forest patch

(Linhart 1989; States et al. 1988). The ability of a squirrel to access these clumps via interlocking canopy corridors becomes increasingly important during winter when snow accumulation can impede ground travel and increase squirrel susceptibility to predation (Stephenson and Brown 1980). Forest restoration based on tree removal potentially could alter the availability of feed trees or reduce access to them by reducing the amount of interlocking canopies.

Given the dependence of tassel-eared squirrels on ponderosa pine, previous studies have suggested that landscape-scale restoration treatments could decrease tassel-eared squirrel density and recruitment if treatments caused overall basal area and number of interlocking canopy trees to fall below critical levels (Dodd et al. 2006). In addition to reducing food and nest site availability, restoration could increase predation by reducing the amount of interlocking canopy that squirrels use as pathways for escaping predators (Austin 1990; Dodd et al. 2003). Although some have suggested that up to 75% of a forested landscape can be treated and still provide suitable squirrel habitat if treatments are applied as a mosaic of patches (Dodd et al. 2006), no studies have examined how individual squirrels respond to forests where restoration treatments have been conducted.

Our objectives were to evaluate seasonal home range and quantify habitat selection by tassel-eared squirrels in a treated landscape. We predicted that squirrels would select home ranges that had a higher than expected proportion of habitat with stand characteristics like those of untreated forest, and that nests would be placed predominantly in untreated areas during both winter and nonwinter seasons.

Materials and Methods

Study area.—The study site was located in and adjacent to the Coconino National Forest's 2,003-ha Fort Valley Experimental Forest (35°16′N, 111°43′W) established in 1909 in northern Arizona. In 1931 study plots within the area were protected from logging, fuel-wood cutting, and other uses, and fire was suppressed in the area (Olberding 2000). Fort Valley is dominated by postsettlement 13- to 41-cm DBH, pole-size ponderosa pines interspersed with groups of mature, presettlement trees and thickets of young saplings. Located at 2,300 m elevation 15 km northwest of Flagstaff, the study area lies within the 3.4-million hectare ponderosa pine belt of north-central Arizona and New Mexico (Mast et al. 1999). From November 2005 to July 2007 total precipitation measured 61 cm, with a total of 240 cm of snowfall, compared to annual mean precipitation of 57 cm (Fulé et al. 2001). Soils within the area are volcanic in origin (Mast et al. 1999).

Contracted thinning and burning restoration treatments on the study sites began in 1998 and initially were completed in fall 2000 (Fulé et al. 2001). Treatments were carried out with mechanical thinning and based on site-specific presettlement tree density ratios. Treatments consisted of no thinning (control), low thinning (3–6 trees left for every presettlement tree or remnant tree material), medium thinning (2–4 trees left), and high thinning (1.5–3 trees left—Abella and Covington 2004). Resulting mean tree density (trees/acre) on treatment blocks ranged from 98 on low-thinning to 69 on medium-thinning and 57 on high-thinning treatments (Fulé et al. 2001). Treatments were carried out on 4 randomly assigned ~17-ha blocks located within a 10-km^2 area that varied in topography from flat to 15% slope (Fulé et al. 2001; Skov et al. 2005). In addition, a combination of these treatments was applied to 4 additional blocks of approximately 40 ha each. Irregularly shaped, untreated areas that followed drainages were left as wildlife corridors throughout the study area. The resulting landscape was spatially heterogeneous, with canopy cover and crown bulk density that varied widely across the area.

Trapping and marking animals.—Research described herein was carried out following the guidelines established by the American Society of Mammalogists for the use of wild mammals in research (Gannon et al. 2007). From November 2005 to December 2005 and in April 2006 we captured squirrels using wire-mesh box traps (model 202; Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with shelled, unsalted, raw peanuts. To incorporate several combinations of forest restoration treatment patches and untreated patches we systematically placed six 4 × 10 trap grids on the study area (Fig. 1A): 2 grids on the western portion (study area A) and 4 on the eastern portion (study area B). All trap grids incorporated some treated and untreated areas, and both study areas were a mosaic of treated and untreated. Traps were spaced 50 m apart, set in the morning, and checked before sunset during weekdays. We trapped for 3 months. We immobilized captured squirrels with an inhalation anesthetic, isoflurane (IsoFlo; Abbott Laboratories, North Chicago, Illinois), and fitted squirrels with a uniquely numbered ear tag (National Band and Tag, Newport, Kentucky) and a 15-g very-high-frequency radiotransmitter (model CHP-3P; Telonics, Mesa, Arizona). In all cases transmitters were <3% of body mass. We determined the sex and weighed each captured squirrel and classified squirrels weighing >550 g as adults (Dodd et al. 2003; Farentinos 1972; Keith 1965). We released squirrels at the capture site after a 15-min anesthetic recovery period.

Radiotracking and range areas.—We used a directional, handheld antenna to track squirrels from December 2005 to July 2007, obtaining visual locations for each squirrel ≥2 times per week. We allocated tracking effort equally across morning, afternoon, and late-afternoon periods. We recorded each animal's location using Universal Transverse Mercator coordinates obtained from a handheld global positioning system unit after the unit achieved an accuracy of ≤8 m and noted if the squirrel was in a nest. In winter 2005–2006 we tracked 7 adults (4 females and 3 males) and 3 juveniles (1 female and 2 males). The following nonwinter (2006) we considered the 1 surviving male juvenile squirrel to be an adult; thus, we tracked 10 adults (5 females and 5 males). For winter 2006–2007 this group of 10 squirrels was reduced by mortality to 9 (5 females and 4 males), and we tracked them for the remainder of the study.

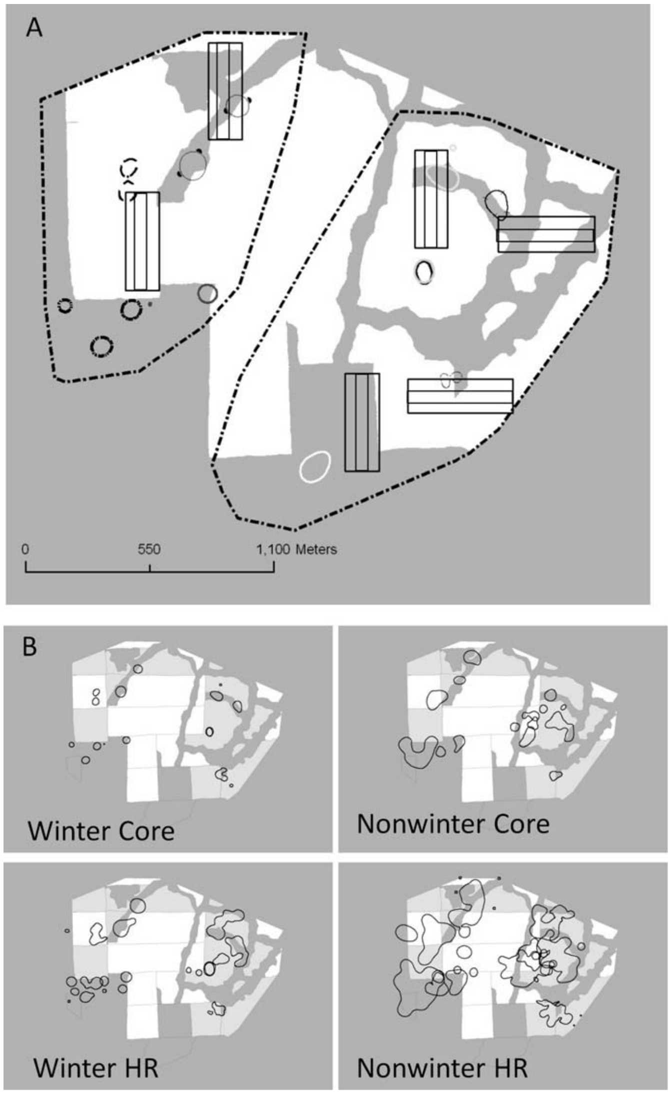

FIG. 1.—A) Core areas used by tassel-eared squirrels in the Fort Valley Experimental Forest, Arizona, during winter. Ellipses with different line characteristics represent the 50% fixed kernel core areas for 10 individual squirrels (some individual squirrels had core areas with >1 focal area and are represented with more than 1 ellipse). Gray areas indicate no treatment, and white indicates some type of tree removal. Black rectangles represent trapping grid locations with long lines representing trap lines. Large, dashed polygons are the minimum convex polygons used to assess habitat availability for the 2 study areas. B) Comparison of core areas and home ranges of the same squirrels across the winter and nonwinter periods. White and lightly shaded areas are treated. Treatments were conducted from 1998 to 2000. Data were collected from November 2005 to July 2007.

We partitioned location data into 2 seasons, winter (1 December–31 March) and nonwinter (1 April–30 November), based on seasonal shifts in squirrel diet. Squirrels rely on inner bark in winter months, and fungi and pine seeds become more important in nonwinter periods (States et al. 1988; Stephenson 1975). For each season (2 winter and 2 nonwinter) we used ArcView 3.3 Home Range Extension (HRE—Rogers and Carr 1998) with a least-squares cross-validation smoothing parameter (Seaman et al. 1999; Seaman and Powell 1996; Worton 1995) to estimate 50% fixed kernel seasonal core areas and 85% fixed kernel seasonal ranges (Worton 1989). We determined the minimum number of locations needed to cause fixed kernel ranges to reach an asymptote (Seaman et al. 1999). Range size stabilized with $\geq$20 locations, and we subsequently used squirrels with $\geq$20 locations/season for further analyses. We used Student's *t*-test blocked by season in JMP 7 (SAS Institute Inc., Cary, North Carolina) to examine differences in core area and seasonal range size between sexes and ages across years. Data were tested for normality using Shapiro–Wilk's test and log-transformed to meet this assumption. We used a Welch analysis of variance (Welch 1938) to test for homogeneity of variance (JMP 7; SAS Institute Inc.,).

Geographic information system layers.—We obtained canopy cover and crown bulk density (the sum weight of foliage and fine branch wood often expressed in kg/m^3) geographic information system vegetation layers from Forest-ERA (Forest Ecosystem Restoration Analysis, Flagstaff, Arizona). Canopy cover is an important parameter for squirrels because interconnected canopies provide travel corridors between feed trees that are more protected from predators than the ground (Dodd et al. 1998, 2003, 2006; Prather et al. 2006); thus we used this layer as an indicator of food accessibility (i.e., as canopy cover increased in an area, so too would a squirrel's ability to access food resources efficiently and safely). Crown bulk density is an estimate of live crown mass, including fine branch wood for individual trees and crown mass density for a specific area (Keyser and Smith 2010). We reasoned that as the amount of live crown mass and branch wood increased so too would the amount of inner bark. We therefore assumed that this parameter would reflect canopy quality, both in terms of amount of food available in the form of fine branches and canopy cover protection from predators and the elements. ForestERA constructed geographic information system layers from the same period as our trapping and telemetry. The canopy cover layer was created from 2005 digital orthophotographs with a 1-m resolution and crown bulk density from fall 2006 (September–October) Landsat TM images (Forest Ecosystem Restoration Analysis) with a pixel resolution of 30 m. We scaled both layers to 60-m pixels from their original resolution and used linear regression analysis between derived crown bulk density and data collected at two hundred forty 0.04-ha plots as an indicator of how accurately derived measures of crown bulk density reflected those on the ground (Fulé et al. 2001). We plotted residuals to confirm that linear regression was appropriate for this analysis. A previous study (Xu et al. 2006) validated the accuracy of canopy cover estimates on this study area. We classified areas as treated if trees had been removed mechanically, regardless of final tree density, and untreated if no trees had been removed mechanically since the 1930s.

Analysis.—Habitat analysis based on the comparison of use versus availability depends on a clearly defined definition of habitat available (Aebischer et al. 1993). We used squirrel behavior to define availability (Buskirk and Millspaugh 2006) and examined use within the hierarchical 2nd, 3rd, and 4th orders (Johnson 1980). We estimated 2nd-order availability at home-range scale (Johnson 1980), based on the relative amounts of treated and untreated area and amount of each canopy cover and crown bulk density category within the minimum convex polygon created from all radiolocations of squirrels captured in each study area (Guthery et al. 2005). We estimated 2nd-order use as either the composition within the 50% fixed kernel core area or within the 85% fixed kernel home range. This analysis therefore compared composition within each individual 50% core area or 85% kernel home range to the composition within the broader study area. We evaluated 3rd- and 4th-order selection (habitat features within the home range—Johnson 1980) by considering the habitat within an individual animal's seasonal 85% fixed kernel home range as available and habitat at each individual radiolocation (3rd order) or nest site location (4th order) as used.

For forest structure habitat characteristics (canopy cover and crown bulk density) at both 2nd- and 3rd-order scales we used compositional analysis (F) to determine if habitat use differed from random ($P < 0.05$), and to rank habitat preference when statistically significant differences existed between availability and use (Aebischer et al. 1993; Aitchison 1986). Compositional analysis avoids the problems of radiolocation serial correlation by using the animal as the sampling unit and addresses the issue of nonindependence by using a log-ratio transformation of habitat proportions (Aebischer et al. 1993). Compositional analysis is recommended for sample sizes $\geq$ 10 individuals (Aebischer et al. 1993); all of our analyses equaled or exceeded this recommended minimum. We followed Bingham and Brennan (2004), substituting values of 0.007 rather than 0.0 for habitat classes where a squirrel was never located. We used chi-square analysis in JMP 7 (SAS Institute Inc.) to determine if use differed from random ($P < 0.05$) for 4th-order selection and for treatment selection at the 2nd and 3rd orders.

Results

Size of range areas.—We captured 18 squirrels, 15 adults (9 females and 6 males) and 3 juveniles (1 female and 2 males). Six of the squirrels were captured in study area A and 12 in study area B, which was proportional to the number of trap grids in each study area. We found no significant differences in range estimates between ages or sexes and therefore pooled all squirrels within a season for each level of analysis. The mean 50% fixed kernel core area for winter (1.10 ha, $SD = 0.68$ ha) was 3 times smaller than nonwinter (3.48 ha, $SD = 2.59$ ha; $t_{10} = 2.85$, $P < 0.001$). Likewise, the mean 85% fixed kernel home range for winter (5.11 ha, $SD =$ 3.38 ha) was >60% smaller than nonwinter (13.81 ha, $SD =$ 6.72 ha; $t_{12} = 3.83$, $P = 0.001$).

Selection.—The geographic information system layers accurately reflected on-the-ground measurements (canopy cover: $r^2 = 0.53$, y = 1.02x; and crown bulk density: $r^2 = 0.71$, y = 0.91x). Squirrels selected untreated areas more than expected from availability when composition of home ranges was compared to that available within each study area in both winter ($\chi^2_1 = 11.51$, $P < 0.001$) and nonwinter ($\chi^2_1 = 3.80$, $P = 0.05$), but when composition of core areas was compared to that within individual home ranges, untreated areas were used more than expected only in winter ($\chi^2_1 = 15.00$, $P <$ 0.001; Fig. 2). In general, squirrel winter core areas were in untreated areas (Fig. 1). Squirrels used areas with canopy cover of 51–75% more than expected and canopy cover of 0–30% less than expected in both seasons (winter: $F_{3,15} = 7.17$, $P < 0.003$; nonwinter: $F_{3,7} = 34.00$, $P < 0.0002$) when canopy composition within home ranges was compared to the composition across the study area, but only in winter ($F_{3,15} =$ 15.28, $P < 0.0001$) when core areas were compared to availability assessed within individual home ranges (Fig. 2). We found no evidence of selection for crown bulk density categories at the home-range (2nd-order) level of selection in any season (winter: $F_{2,16} = 1.72$, $P > 0.21$; nonwinter: $F_{2,8} =$ 0.55, $P > 0.59$) Likewise, we found no support for selection for treated compared to untreated areas (winter: $\chi^2_1 = 0.93$, $P = 0.33$; nonwinter: $\chi^2_1 = 1.04$, $P = 0.31$), or specific canopy cover (winter: $F_{3,15} = 0.74$, $P > 0.19$; nonwinter: $F_{3,7} = 0.96$, $P > 0.96$) or crown bulk density (winter: $F_{2,16} = 0.89$, $P > 0.40$; nonwinter: $F_{2,8} = 1.04$, $P > 0.40$) categories in either season when selection was based on individual radiolocations (3rd-order selection).

Although squirrels placed nests in treated and untreated areas as expected based on availability (winter: $\chi^2_1 = 1.62$, $P = 0.20$; nonwinter: $\chi^2_1 = 2.63$, $P = 0.10$), selection for canopy cover and crown bulk density occurred within these categories during both winter and nonwinter seasons (Fig. 3), and the availability of these categories was reduced by treatment (Fig. 4). During winter, squirrels selected nest placement sites (4th-order selection) with canopy cover ($\chi^2_1 = 7.88$, $P = 0.005$) and crown bulk density ($\chi^2_1 = 4.53$, $P =$ 0.03) that differed from availability, placing the majority of nests in areas with 51–75% canopy cover and 0.06–0.08 kg/m^3 crown bulk density. For nonwinter, squirrels again selected nest sites with canopy cover ($\chi^2_1 = 6.23$, $P = 0.01$) and crown bulk density ($\chi^2_1 = 4.86$, $P = 0.03$) that differed from availability. However, for this season, squirrels selected areas with canopy cover of 76–100% and crown bulk density of 0.06–0.08 kg/m^3.

Overall, tassel-eared squirrels in our study disproportionately used areas that had either not been treated or had received forest treatments that resulted in higher canopy cover when compared to other treatments. Squirrels underutilized areas that had low canopy cover and crown bulk density whether they occurred as natural openings in untreated forest or as heavily thinned areas.

Discussion

Our findings are consistent with other studies that found that areas with high basal area and high canopy cover supported

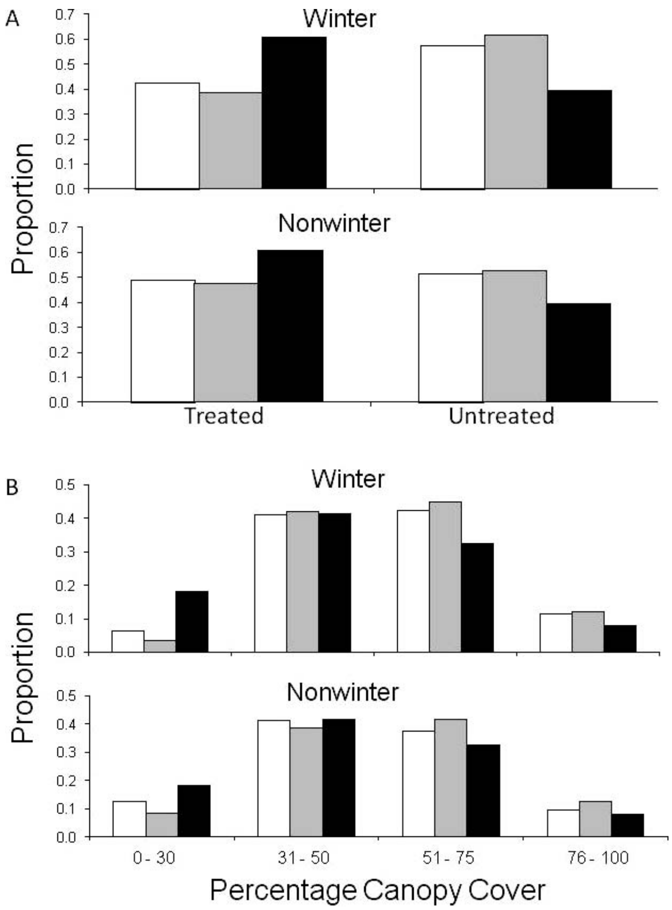

FIG. 2.—Second-order habitat selection (see ''Materials and Methods'' for definition) by tassel-eared squirrels in the Fort Valley Experimental Forest, Arizona, during winter and nonwinter periods based on A) treated versus untreated areas and B) canopy cover categories. White bars indicate the proportional use of each habitat category at the level of squirrel home range, gray bars indicate proportional use at the level of squirrel core area, and black bars indicate habitat proportion available. Treatments were conducted from 1998 to 2000. Data were collected from November 2005 to July 2007.

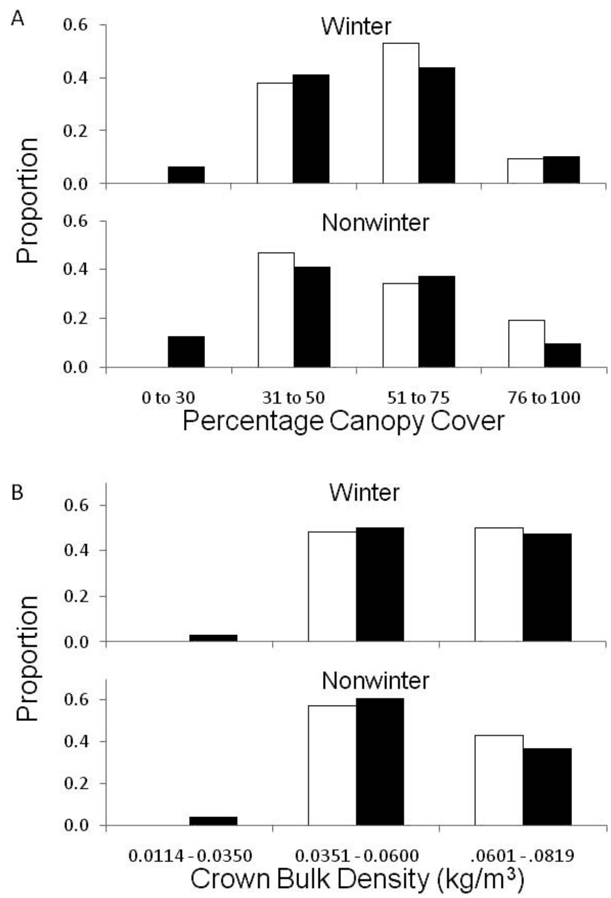

FIG. 3.—Fourth-order habitat selection (see ''Materials and Methods'' for definition) by tassel-eared squirrels in the Fort Valley Experimental Forest, Arizona, during winter and nonwinter periods based on A) canopy cover and B) crown bulk density categories. White bars indicate the proportional use of each habitat category, and black bars indicate habitat proportion available. Treatments were conducted from 1998 to 2000. Data were collected from November 2005 to July 2007.

higher squirrel densities (Dodd et al. 2006; Patton et al. 1985; Trowbridge and Lawson 1942). Although tassel-eared squirrels selected for untreated patches in both seasons, this pattern was strongest during winter when squirrels selected untreated forest patches as core use areas. Squirrels placed nests in areas with high canopy cover and crown bulk density in both untreated and treated areas. We hypothesize that these areas of higher canopy cover and greater bulk density provided squirrels with feed trees with interlocking canopies and nest locations that had thermal and structural properties necessary for buffering against wind and temperature extremes during this critical winter period (Golightly and Ohmart 1978). Snowfall during both years of our study (113 cm in 2005–2006 and 129 cm in 2006–2007) was approximately one-half of the 30-year average (277 cm; National Climatic Data Center, www.ncdc.noaa.gov/oa/ncde.html, accessed 4 August 2009), suggesting that our results are representative of relatively mild winters. In winters with heavier snowfall interlocking canopies might become more important as escape routes and as travel pathways to access feed trees.

Although squirrels underutilized treated areas and areas with low canopy cover based on availability, squirrels still used these areas during both winter and nonwinter seasons, and some squirrels had core ranges that fell entirely within treated areas. This might have been driven in part by squirrels using more open sites because trees in these areas have greater access to nutrients and water and thereby increase cone production during the summer (Dodd et al. 1998). In addition, treatment prescriptions in our study area varied both across and within treatments because they were based on site-specific historical evidence of presettlement conditions. As a result, treated areas varied considerably in tree density and canopy cover. Although the total area with ranges of canopy cover and crown bulk density that squirrels favored was lower overall in treated areas, some remained that squirrels likely were able to exploit (e.g., nest placement within treatments). In this respect our study is different from those that studied squirrel response in large areas receiving a single treatment prescription that reduced all areas to the same specific stem density, diameter at breast

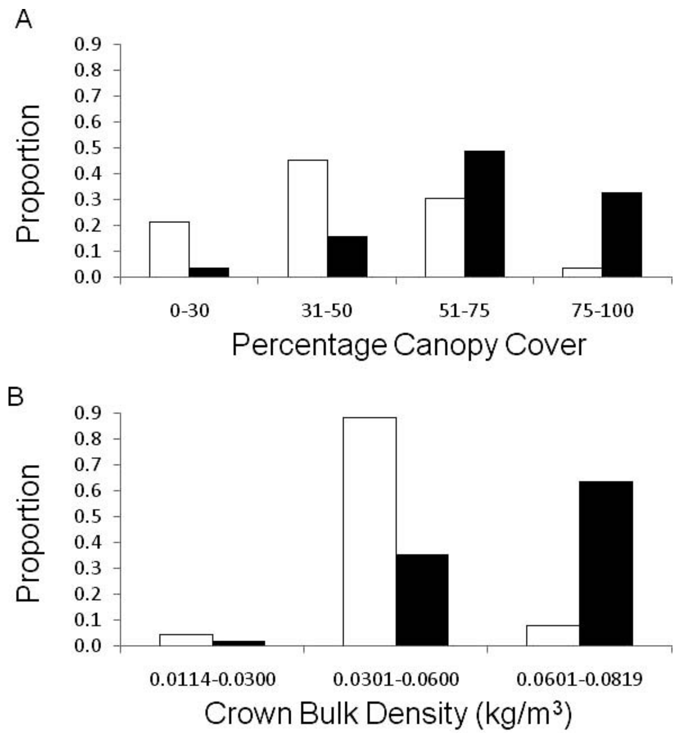

FIG. 4.—Proportion of A) canopy cover and B) crown bulk density available to squirrels in treated (white bars) and untreated (black bars) areas at the Fort Valley Experimental Forest in Arizona. Treatments were conducted from 1998 to 2000.

height, or canopy cover value (Patton et al. 1985; Pederson et al. 1987; Trowbridge and Lawson 1942). An important caveat of our study was that treated areas were surrounded by untreated areas and might have been too small ($\bar{X}$ = 14 ha) to include enough individual home ranges (~14 ha per individual) to assess the effects of large-scale treatment, a situation not uncommon in experimental tests of the impacts of forest restoration (Block et al. 2001). However, the disproportionate use of higher density, untreated areas, especially in winter, by the majority of our squirrels suggests that without retention of untreated or higher tree density areas, squirrel abundance likely would decline in areas of extensive restoration treatments.

Current views that ponderosa pine forests were historically more open and park-like (Allen et al. 2002; Cooper 1960; Covington and Moore 1994; Mast et al. 1999; White 1985), combined with consistent findings that squirrel density and recruitment are linked to high canopy closure (Dodd et al. 1998, 2006; Patton 1975, 1984), suggest that presettlement squirrel populations were likely lower than they are currently. Restoration treatments designed to recreate presettlement conditions might reduce squirrel populations. Initial mechanical thinning can create tree densities and spatial patterns similar to those present during presettlement but cannot replace large, old-growth trees removed by historical and contemporary commercial logging that could be of considerable importance to squirrels. Squirrels are a management indicator species, perform important ecosystem functions such as dispersal of mycorrhizal fungal spores (Kotter and Farentinos 1984), act as prey for sensitive species (e.g., northern goshawk—Reynolds et al. 1992), and are a popular small game species. Where management goals include maintaining squirrel populations at or near current levels, our results suggest that retention of untreated areas or incorporation of treated areas with high canopy cover should be considered. Site-specific restoration treatments commonly include extensive field surveys for evidence of presettlement trees. These efforts could be augmented to benefit squirrels by identifying feed and nest trees to be retained after treatment.

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